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Linking seed fate to natural dispersal patterns: factors affecting predation and scatter-hoarding of *Virola calophylla* seeds in Peru

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Abstract: Natural seed deposition patterns and their effects on post-dispersal seed fate are critical in tropical tree recruitment. Previous research showed that the key dispersal agent of the neotropical tree, *Virola calophylla*, is the spider monkey (*Ateles paniscus*). Spider monkeys generate a heterogeneous seed deposition pattern because they scatter-disperse seeds diurnally, whereas they clump-disperse seeds at their sleeping sites. The recruitment consequences of this pattern were investigated using manipulative experiments and observations. Scatter-hoarding by spiny rats (*Proechimys* spp.) caused little rearrangement of the initial seed deposition pattern because they moved seeds only short distances. Seed survival to the seedling stage depended negatively on conspecific seed density and positively on the distance from the nearest adult *V. calophylla* female. These effects were likely mediated by two important seed predators, spiny rats and beetles (Scolytidae). Furthermore, spider monkeys' seed deposition patterns influenced seed survival. Scatter-dispersed and experimentally dispersed seeds had the highest survival. Conversely, clump-dispersed seeds at sleeping sites, which are far from *V. calophylla* females, and non-dispersed seeds had equally low survival, suggesting that conspecific density- and distance-dependence acted independently and did not explain all variation in seed survival. Instead, other characteristics of the seed deposition pattern, such as the multi-specific assemblage of seeds at sleeping sites, also affected post-dispersal seed fates.

Resumen: La conexión entre el patrón natural de dispersión de semillas con el destino después de la dispersión es clave para el reclutamiento de árboles tropicales. Mediante experimentos y observaciones se investigó esta conexión utilizando el árbol neotropical *Virola calophylla* (Myristicaceae). *Ateles paniscus* (maquisapa), el principal dispersor de sus semillas, genera un patrón de deposición heterogéneo. Durante el día las semillas son depositadas de manera esparcida mientras que en los dormitorios las semillas son depositadas de manera agregada. En este estudio se encontró que los roedores espinosos (*Proechimys* spp.) almacenaron semillas individuales debajo de la hojarasca, sin embargo estos no alteraron el patrón de dispersión ya que las semillas fueron transportadas distancias cortas y la tasa de predación fue alta. Se encontró que la tasa de sobrevivencia hasta la etapa de plántula tuvo una relación negativa con la densidad de las semillas y una relación positiva con la distancia al árbol hembra de *V. calophylla* mas cercano. Estos efectos sucedieron por medio de roedores espinosos y coleópteros (Scolytidae), predadores importantes de las semillas de *V. calophylla*. Adicionalmente, el patrón de deposición de los maquisapas influyó la sobrevivencia de las semillas. Tanto las semillas dispersadas por los maquisapas como las dispersadas experimentalmente tuvieron la tasa de sobrevivencia más alta. Por el contrario, tanto las semillas depositadas en los dormitorios, usualmente lejos de hembras de *V. calophylla*, como las semillas que cayeron debajo del árbol hembra tuvieron bajos niveles de sobrevivencia. Estos resultados sugieren que tanto la densidad como la distancia tuvieron efectos independientes y no explicaron toda la variación observada en la sobrevivencia de semillas. Por el contrario, otras características de la deposición de semillas tales como la riqueza de especies de la comunidad de semillas en los dormitorios también afectaron el destino de las semillas después de dispersadas.

Key Words: *Ateles paniscus*, Myristicaceae, Perú, *Proechimys*, scatter-hoarding, Scolytidae, seed dispersal, seed predation, spider monkeys, tropical floodplain forest, *Virola calophylla*

INTRODUCTION

The spatial pattern of seed deposition has implications for plant recruitment, particularly the fates of seeds as they make the transition into the seedling stage (Nathan &

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Muller-Landau 2000). Post-dispersal seed fate, in turn, plays an important role in the demography, spatial distribution and coexistence of plant species (Hubbell 1980, Hulme 1998, Janzen 1971). Thus, quantifying natural seed deposition patterns and determining how they shape variation in post-dispersal seed fate is critical to understanding the structure and dynamics of tropical forest communities.

Seeds can experience different fates mediated by a variety of agents. After dispersal by birds and mammals or falling from a parent, seeds can be preyed upon or dispersed once again. Seed predators can have a particularly strong impact on plant populations. Indeed, it is often observed that the seed to seedling transition is the strongest demographic filter for most plants (Harper 1977), although among tropical trees, later life stages can also be influential (Alvarez-Buylla & Martinez-Ramos 1992). However, some granivores, particularly rodents, not only consume seeds, but also cache them (Price & Jenkins 1986). Some seeds buried in caches are later recovered and eaten, but others may survive unrecovered. For cached seeds that survive, the effect is to further rearrange the seed deposition pattern, which can be beneficial if it results in the dispersal of seeds to uncolonized sites or in higher survival relative to uncached seeds (Forget *et al.* 1998, Wenny 1999). Thus, these granivores may act as both mutualists and seed predators (Longland *et al.* 2001).

Much experimental work has been done to quantify the effects on post-dispersal seed fate of biotic and abiotic factors, such as predators' responses to conspecific seed density or distance from a parent tree and effects of leaf litter on germination (Forget *et al.* 2000, Hammond *et al.* 1999, Molofsky & Augspurger 1992, Schupp 1988a). However, relatively fewer studies have combined experiments with quantification of natural seed deposition patterns to understand the consequences for seed fates (for examples, see Augspurger & Kitajima 1992, Fragoso 1997, Nathan *et al.* 2000, Vander Wall 1994, Wenny 2000). Consequently, although particular factors may be identified in an experimental context as affecting seed fates, their relevance for fates of naturally dispersed seeds and for how these factors interact in natural dispersal systems remains un-illuminated by purely experimental approaches. Thus, combining experimentation with observations of natural dispersal patterns and seed fates can be more informative than experiments alone because a combined approach reveals the mechanisms by which dispersal agents directly affect the fates of seeds they disperse. This is particularly important for plants dispersed by animals because they frequently generate spatially aggregated patterns of seed deposition as a result of their behaviour and movement patterns (Schupp *et al.* 2002).

Here I present the results of a combination of manipulative experiments and natural observations that investigated post-dispersal fates of seeds of *Virola calophylla* (Myristicaceae), a neotropical nutmeg tree, at Cocha Cashu Biological Station (CCBS) in floodplain forest in Peru. At CCBS, *V. calophylla* is dispersed by birds and one primate, the spider monkey (*Ateles paniscus*) (Russo 2003). Spider monkeys disperse more seeds than all avian dispersal agents combined (Russo 2003). Because of variation in their movements and behaviours, they generate a heterogeneous seed shadow characterized by both scattered and clumped dispersal patterns (*sensu* Howe 1989, Russo & Augspurger 2004). When spider monkeys defecate seeds during diurnal resting or foraging (in-transit dispersal sites), seeds are dispersed in a scattered pattern, i.e. distributed at widely spaced intervals in the forest and in small areas having low densities of seeds. In contrast, at their sleeping sites many monkeys congregate at nightfall and in the morning defecate large numbers of seeds. Seed dispersal at sleeping sites therefore produces a clumped pattern of dispersal because sleeping sites are relatively larger in area, accumulate higher densities of seeds, and are more frequently re-used, relative to in-transit sites (Russo & Augspurger 2004).

The objective of this study was to investigate the consequences that natural seed deposition patterns generated by spider monkeys have for fates of *V. calophylla* seeds. First, seed predators and seed-caching agents were identified. Second, seed survival and germination among non-dispersed seeds (seeds falling below the parent), seeds dispersed by spider monkeys at their sleeping and in-transit sites, and experimentally dispersed seeds (intended to mimic dispersal by birds) were compared. Third, significant sources of variation in seed mortality were identified and their relative strengths estimated, including the effects of density- and distance-dependence and the environmental characteristics at sites of seed deposition.

METHODS

Study site and species

This study was conducted from July 2000 to December 2001 at Cocha Cashu Biological Station (CCBS) in Manú National Park, Perú (11°54'S, 71°18'W, elevation c. 400 m asl). Annual rainfall at CCBS averages c. 2000 mm, with most precipitation falling between October and April (Terborgh 1983). This study was conducted in approximately 300 ha of mature floodplain forest at CCBS. Community-wide fruit production has two phenological peaks annually, one near the beginning (November–December) and one near the middle (February) of the rainy season (Terborgh 1983). This

site has been described in detail in Terborgh (1983) and Gentry (1990).

Species of *Virola* have been used as model systems for studying seed dispersal (Forget & Milleron 1991, Howe 1981, Howe *et al.* 1985). *Virola calophylla* is a dioecious, shade-tolerant, canopy tree in lowland moist tropical forests of South America (Rodrigues 1980). At CCBS *V. calophylla* ripens fruit from early to mid-September to December. The fruit of *V. calophylla* is a bivalved, dark green capsule that opens upon ripening to expose a single seed with a bright red, oily aril. The seed (length: 17.0 ± 1.8 mm, $n = 98$; fresh mass: 1.4 ± 0.5 g, $n = 108$; $\bar{x} \pm \text{SD}$) accounts for most of the volume of the diaspore.

At CCBS seeds of *V. calophylla* are dispersed by at least 17 bird species and one primate, the spider monkey, *Ateles paniscus* (Russo 2003). Avian dispersers include toucans and araçaris (Ramphastidae), trogons, (Trogonidae) and guans (Cracidae). Trogons ingested 1–2 seeds per visit, whereas guans, toucans and araçaris ingested from 1–30 seeds per visit (Russo 2003). These birds either defecate (guans) or regurgitate seeds intact. Spider monkeys dispersed 92% of dispersed seeds (Russo 2003). They ingested up to 104 seeds in a visit and defecated them intact. They are highly frugivorous, forage primarily in the canopy and subcanopy and have large home ranges (150–230 ha; Symington 1987).

Seed predation and caching

Many mammals at CCBS both prey upon and cache seeds, including agoutis (*Dasyprocta* spp., Smythe 1978), acouchies (*Myoprocta* spp., Jansen *et al.* 2002, Morris 1962), spiny rats (*Proechimys* spp., Adler & Kestell 1998, Forget 1991) and squirrels (*Sciurus* spp., Terborgh 1986). The species that prey upon or cache (scatter- or larder-hoard) seeds of *V. calophylla* were identified by placing seeds marked with flagging tape inside tracking stations (Wemmer *et al.* 1996). Scatter-hoarded seeds are defined as those buried under a few centimetres of soil or simply under leaf litter, whereas larder-hoarded seeds are buried to depths greater than *c.* 10 cm (Vander Wall 1990). Secondary dispersal by dung beetles of *V. calophylla* appears to be minimal at this site (Andresen 1994, E. Andresen, *pers. comm.*), so it was not addressed in this study.

Each tracking station was constructed in an area relatively free of vegetation by digging out *c.* 3–5 cm of soil from a 1-m² area. The bottom of the cleared-out area was smoothed and the area was filled with fine, dry, sifted sand from a nearby beach along the Manú River. Freshly fallen seeds were collected from beneath multiple fruiting *V. calophylla* trees distant from the study area. The arils were manually removed from the seeds and damaged seeds were discarded. The effect of presence or absence

of aril on seed predation or caching is likely minimal, as indicated by the results of a limited pilot study (S. E. Russo, unpubl. data). The intact seeds from the multiple source trees were bulked and those to be experimentally dispersed were selected at random from the bulked seeds. A 30-cm length of unwaxed dental floss with a short (*c.* 4 cm) piece of flagging tape tied to one end was glued with quick-set epoxy to each seed. Other studies found no effect of this marking technique on the probability of seed removal (Brewer & Rejmánek 1999, Forget & Wenny 2004, Forget *et al.* 2000, Schupp 1988b, Wenny 2000).

Three tracking stations were placed under each of two fruiting *V. calophylla* trees ($n = 6$) and three were placed at each of two randomly selected locations in the forest > 75 m from any *V. calophylla* trees ($n = 6$), for a total of 12 tracking stations. Initially, six flagged seeds were placed in each 1-m² tracking station. After all six seeds disappeared from a tracking station, they were replaced with a new batch of six, for a total of 12 seeds per station ($N = 144$). This design simulated the natural availability of seeds under fruiting females and at sites of seed dispersal by spider monkeys. Placement of seeds spanned the beginning to early middle of the fruiting season of *V. calophylla* in 2000. Because one seed was lost from the experiment due to human error, the sample size was 143 seeds.

Tracking stations were checked and the area in a 20-m radius surrounding them was searched daily until all seeds had been cached or eaten. The distance from the station of origin to the seed's location of cache or predation was recorded. At each check, all prints recognizably produced by a vertebrate in each station were sketched, measured (length and width) and identified using the descriptions and sketches in Reid (1997) and Emmons & Feer (1990). Sand was smoothed and cleared of old prints and debris after being checked. When only cached seeds remained, they were checked approximately twice a month for the first 2 mo and then 5 mo and 6 mo later.

Non-dispersed and naturally and experimentally dispersed seeds

Ten adult female trees (> 10 cm diameter at breast height) bearing fruit in the study area in 2000 were randomly selected. Trees with very small crop sizes were excluded because the goal was to obtain a large enough sample of seeds to estimate seed survival rate. Beneath each tree, 3–12 1-m² fruit traps were located randomly using methods described in Russo (2003). Next to each trap, a quadrat (0.5 × 0.5 m) was located. At each weekly emptying of traps, one quarter of all seeds in the trap were individually coded using coloured paint and placed in the quadrat. Painting seeds is a commonly used technique to track seed fates (Augsburger & Kitajima

1992, Gurnell 1984). One seed naturally fallen into the quadrat and not part of the experiment was removed for each painted seed added to the quadrat. This procedure allowed the exact starting date of exposure to terrestrial predators to be known, being the date the seed was placed into the quadrat; this date ranged from early to late in the *V. calophylla* population's fruiting season (c. 4 mo). No more than 10 seeds per quadrat per week were coded and placed for monitoring. The range of the total number of monitored seeds in a quadrat was 1–42, for a total of 638 seeds.

Individual spider monkeys that fed in *V. calophylla* trees were followed to map the locations where spider monkeys defecated *V. calophylla* seeds at sleeping and in-transit sites. When spider monkeys defecated *V. calophylla* seeds, the boundary of the area receiving freshly defecated seeds was delineated. This area was divided into quadrats (0.5×0.5 m), which were aligned to give the minimum number of quadrats. Each seed was contained within one quadrat, but quadrats could contain more than one seed. All freshly defecated seeds of *V. calophylla* were counted and individually coded using coloured paint. Within each quadrat, the total number of *V. calophylla* seeds and seeds of other species (including older, previously defecated, as well as freshly defecated, seeds) was recorded to estimate the densities of dispersed seeds at these sites. The date on which each seed was dispersed was recorded; dates spanned the *V. calophylla* population's fruiting season. At sleeping sites ($n = 14$ sites), the range of the number of quadrats per site was 1–42, with 1–23 seeds per quadrat, for a total of 434 naturally dispersed seeds monitored at sleeping sites. At in-transit sites ($n = 14$ sites), the range of the number of quadrats per site was 1–8, with 1–6 seeds per quadrat, for a total of 77 naturally dispersed seeds monitored at in-transit sites.

Seeds of *V. calophylla* were experimentally dispersed to mimic locations of seeds regurgitated by birds. Seeds were selected randomly from the bulked seeds, as described above. Paired quadrats (0.5×0.5 m) were placed 30 m apart from each other, starting from a randomly selected location. Each pair consisted of a high- (six seeds) and low-density quadrat (one seed). A total of 132 quadrats (66 pairs; a total of 425 seeds) were placed. Random placement of single quadrats mimicked the more scattered seed deposition pattern that many bird species dispersing *V. calophylla* are expected to produce at larger spatial scales (Howe 1989). Placement of one or six seeds per quadrat is representative of the possible numbers of seeds dispersed underneath a perch for bird species that disperse *V. calophylla* at CCBS. Seeds were uniquely coded as described above. Experimentally dispersed seeds were placed at temporally staggered intervals, mimicking natural dispersal. The date on which each seed was placed in its quadrat was recorded; dates spanned the *V. calophylla* population's fruiting season. In each quadrat,

the numbers of seeds of *V. calophylla* and of other species there before experimental placement of *V. calophylla* seeds were recorded. An additional set of 36 pairs of protected quadrats ($n = 72$) was also established because heavy seed predation by mammals was anticipated. A 15-cm tall cubical cage made of 7-mm-mesh wire screening was fitted over each quadrat. The sides of the cage were embedded into the soil to a depth of c. 3–5 cm. The top of each cage was closed, but had a small door that could be opened and closed to allow seed monitoring. Cages allowed entry of all but the largest invertebrates, but excluded mammals. Thus, protection of seeds allowed estimation of the percentage of seeds germinating and their mean time to germination in the absence of mammalian predators and of the amount of seed predation by mammals and invertebrates.

Unprotected (non-dispersed and naturally and experimentally dispersed) and protected (experimentally dispersed) seeds were censused every 2 and 3 wk, respectively, over a period of 15 mo to evaluate seed survival and germination. Seeds were categorized as (1) intact, but not germinated, (2) removed (seed not found in quadrat), (3) seed present, but preyed upon (evidence of penetration of seed coat by a predator or remains of seed coat with painted code found), (4) seed present, with insect hole in coat, but otherwise intact or (5) germinated. For seeds in categories 3 and 4, the damage was described and the probable identity of the organism responsible (i.e. insect or mammal) was recorded. Germinating seeds were identified by the protrusion of the radicle from one tip of the seed or from presence of a seedling with a painted seed still attached or very close by. Preliminary studies indicated that *V. calophylla* seeds can germinate and establish seedlings with two leaves in 13 mo.

At all quadrats, six site characteristics potentially affecting seed predation, germination and seedling survival were measured. These characteristics were chosen because of their potential to influence the foraging behaviour of seed predators (Lambert & Adler 2000, Price & Jenkins 1986), presence of other natural enemies (Connell 1971, Janzen 1970) and ability of germinating seeds to emerge through leaf litter (Molofsky & Augspurger 1992). Stem density was the number of stems of plants < 50 cm tall within a 1-m radius of the centre of the quadrat. Leaf litter depth was the number of leaves pierced by a 10-cm nail thrust into the soil once in each quadrat when the seeds in that quadrat were dispersed. The densities of seeds of *V. calophylla* and of other species in each quadrat were recorded. The distance of each quadrat to the nearest adult female *V. calophylla* tree was calculated based on mapped locations of quadrats and trees. Dispersal date was the date on which a seed was either experimentally or naturally dispersed into its quadrat.

Statistical analyses

Variation in per capita seed survival to the seedling stage was analysed using generalised linear models (McCullach & Nelder 1989) employing a binomial error distribution and logit link function (logistic regression) in SAS PROC GENMOD (SAS Institute 2000a, Stokes *et al.* 2000). In these analyses the response variable was binomial (seed was alive or dead; $n = 1574$ unprotected seeds, $n = 252$ protected seeds). Seeds were considered alive if they were intact or germinating (categories 1 and 5). A seed was also considered alive if its seed coat had only one hole made by a scolytid beetle, as such seeds maintained the potential to germinate. Otherwise, seeds were considered dead (categories 2–4). The data were analysed at seed ages of 16 and 38 d and at the end of the study to assess temporal variation in seed survival. Ages of seeds at the end of the study varied because seeds were dispersed on different dates, but ranged from 13–15 mo. Two sets of analyses were performed. In one set a categorical predictor variable (dispersal site type) tested for variation in per capita seed survival among non-dispersed, spider monkeys' sleeping and in-transit and experimental site types. Likelihood ratio tests (LRT) were used to test for differences in per capita survival between pairs of site types based on odds ratios. The odds ratio compares whether the probability of an event (here, seed survival of a seed to one of the three times) is the same (odds ratio equal to one) for the compared groups (Stokes *et al.* 2000).

The second set of analyses tested the effects on per capita seed survival of the six continuous predictor variables describing site characteristics. Analyses of deviance using LRT were used to determine the best-fit main-effects model. Specifically, LRT evaluated the change in the variance in the dependent variable that was explained when a factor was added into the model, compared to that explained without that factor (Stokes *et al.* 2000). Type III tests were used because their probabilities are independent of the order in which the factors are entered into the model (SAS Institute 2000b) and because they are recommended for unbalanced data (Shaw & Mitchell-Olds 1993). Odds ratios were used to estimate the strength of effects of each predictor variable on per capita survival, corresponding to a unit increase in a predictor variable (SAS Institute 2000b).

RESULTS

Of the seeds experimentally placed into tracking stations, 98% ($n = 140$ of 143) of seeds or their flagging tape were found. All of these seeds were eventually eaten after 11 mo, most within one to a few days of being placed. Eighty-six per cent of seeds (123 of 143) placed in tracking

stations were eaten and never scatter-hoarded. Twelve per cent of seeds (17 of 143) in tracking stations were scatter-hoarded at least once, but all were later eaten. Scatter-hoarded seeds were cached singly under the leaf litter and sometimes buried in the soil to a depth of c. 1–2 cm. No evidence of larder-hoarding (burial of groups of seeds > 10 cm below the soil surface) was found.

With the exception of one, all discernable tracks in tracking stations that were associated with seed predation or scatter-hoarding events were identified as having been made by spiny rats (*Proechimys* spp., Rodentia: Echimyidae; front foot width 1.5–2.0 cm, length 1.7–1.9 cm; hind foot width 1.8–2.2 cm, length 2.5–2.7 cm). Thus, at least 48% of seed fates (69 of 143) were associated with spiny rat tracks in tracking stations. This genus-level identification was confirmed by tracks made on sand of a locally live-trapped spiny rat. In the only case in which tracks associated with seed predation were not made by spiny rats, they were identified as those of the agouti (*Dasyprocta variegata*, Rodentia: Dasyproctidae).

All scatter-hoarded seeds were dispersed less than 5 m from their tracking station of origin ($\bar{x} = 2.5$ m, median = 2.1 m, SD = 1.4 m, $n = 16$). This distance is not far enough to be dispersed from under most *V. calophylla* tree crowns (crown diameter $\bar{x} = 7.3$ m, SD = 2.3 m, $n = 30$ trees), unless the seed is near the edge of the crown. Most seeds were moved < 1 m from their station of origin to be eaten ($\bar{x} = 1.4$ m, median = 0.54 m, SD = 2.2 m, $n = 93$).

Seed predation of unprotected seeds was extensive. A total of 99% ($n = 1557$ of 1574 seeds) of unprotected naturally and experimentally dispersed seeds did not survive to establish seedlings by the end of the study; 60% had been preyed upon after only 16 d. Most seeds were removed from quadrats with no direct evidence of predation. For many seeds, however, mammal predation was evident from remains consisting of bits of chewed endosperm or pieces of painted seed coat in and near quadrats. Two genera of scolytid beetles were also important predators of *V. calophylla* seeds (*Coccotrypes* and *Spermophthorus*; Scolytidae: Coleoptera). Adult beetles were observed to make holes in the seed coats. Larvae developed inside the seed and consumed the endosperm, often killing the embryo in the process. Seeds attacked by beetles also died of what appeared to be a pathogen infection of the endosperm. Several seeds survived to germinate, but later died as a result of herbivory or of what appeared to be a pathogen infection of the young radicle, which spread to the endosperm.

Per capita seed survival differed among dispersal site types (non-dispersed, spider monkey sleeping and in-transit sites and sites of experimental dispersal) at all three times ($n = 635$ seeds alive at 16 d, $\chi^2 = 121$, $df = 3$, $P < 0.0001$; $n = 409$ seeds alive at 38 d, $\chi^2 = 161$, $df = 3$, $P < 0.0001$; $n = 17$ seeds alive at end of the study,

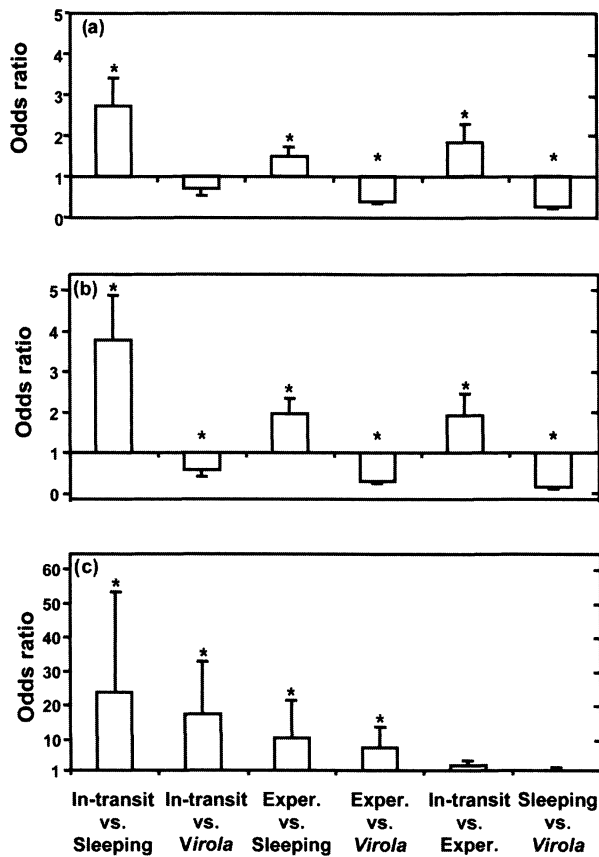


Figure 1. Odds ratio estimates (± 1 SE) for pair-wise comparisons of site types at three time points. Experimental sites are abbreviated as Exper. Odds ratios for a particular comparison significantly different from one at $P < 0.05$ are denoted with an asterisk above the bar. (a) Seed age of 16 d; (b) Seed age of 38 d; (c) Seed age 13–15 mo (end of the study). Note change in vertical scales. Odds ratios > 1 indicate higher survival in the first site of the pair; odds ratios < 1 indicate lower survival in the first site of the pair.

$\chi^2 = 20.4$, $df = 3$, $P < 0.0001$). However, the direction of difference between pairs of site types, as indicated by odds ratios, changed with time (Figure 1). Seed survival was consistently high at in-transit sites, particularly relative to sleeping sites. Survival to 16 d was high beneath *V. calophylla* females and remained high up to 38 d following dispersal. However, by the end of the study, seeds beneath *V. calophylla* females and at sleeping sites had equally poor odds of surviving; their odds were significantly lower than at either in-transit or experimental sites. Seeds beneath *V. calophylla* females and at sleeping sites had 17 and 24 times worse odds of surviving, respectively, than seeds at in-transit sites, and 10 and 8 times worse odds of surviving, respectively, than seeds at experimental sites (Figure 1). Seed survival at in-transit and experimental sites did not differ significantly.

The site characteristics that were significant predictors of per capita seed survival and the directions of their effects also varied in time (Table 1). The average number of stems at quadrats was 9.0 (range = 1–34), but it had

Table 1. Site characteristics significantly affecting per capita survival to seedling establishment of non-dispersed, naturally dispersed and experimentally dispersed *Virola calophylla* seeds. Only factors retained in the optimal model from an analysis of deviance are shown. Degrees of freedom equal one for all tests. Odds ratios significantly different from one (95% confidence limits (CL)) indicate the increase (> 1) or decrease (< 1) in survival odds with a unit increase in the predictor variable. Units for each variable are in parentheses.

Characteristic (units)	χ^2	Probability	Odds ratio (95% CL)
Seed age: 16 d			
Leaf litter depth (leaf layer)	19.6	< 0.0001	1.19 (1.10–1.29)
<i>V. calophylla</i> seed density (seed)	66.0	< 0.0001	1.08 (1.06–1.10)
Distance from <i>V. calophylla</i> female (m)	25.7	< 0.0001	0.99 (0.98–0.99)
Non- <i>V. calophylla</i> seed density (seed)	55.8	< 0.0001	0.97 (0.96–0.98)
Seed age: 38 d			
<i>V. calophylla</i> seed density (seed)	19.4	< 0.0001	1.04 (1.02–1.06)
Distance from <i>V. calophylla</i> female (m)	44.0	< 0.0001	0.99 (0.98–0.99)
Non- <i>V. calophylla</i> seed density (seed)	37.4	< 0.0001	0.96 (0.94–0.98)
Date of dispersal (d)	6.85	0.0088	1.01 (1.01–1.02)
Seed age: 13–15 mo			
<i>V. calophylla</i> seed density (seed)	12.1	0.0005	0.77 (0.62–0.94)
Distance from <i>V. calophylla</i> female (m)	8.36	0.0038	1.01 (1.01–1.02)
Date of dispersal (d)	11.2	0.0008	1.08 (1.03–1.13)

no statistically significant effect on seed survival. On average quadrats had 2.5 layers of leaves (range = 0–10). Deeper leaf litter increased the probability a seed would survive to 16 d, but the magnitude of this effect decreased until it became non-significant by the end of the study (Table 1). The density of *V. calophylla* seeds in a quadrat averaged 3.2 seeds (range = 1–40). The average density underneath parent crowns tended to be higher than that at sleeping sites, which tended to be higher than that at in-transit sites (Figure 2). The distance of quadrats from the nearest female *V. calophylla* tree (excluding those underneath females) averaged 45.8 m (range = 0–240) and was significantly longer for in-transit relative to sleeping sites (analysis of variance, $F(2, 33) = 4.04$, $P = 0.027$, adjusted for multiple comparisons using Tukey–Kramer method). The density of *V. calophylla* seeds and the distance from the nearest female *V. calophylla* tree both significantly affected per capita seed survival at all three times (Table 1). At 16 and 38 d, seeds in quadrats with higher seed density and closer to a female conspecific had a higher probability of surviving. Nonetheless, by the end of the study, this effect reversed, and seed survival displayed negative density-dependence and positive distance-dependence (Table 1). This change in the direction of effects for these two factors is consistent with the early high odds of survival

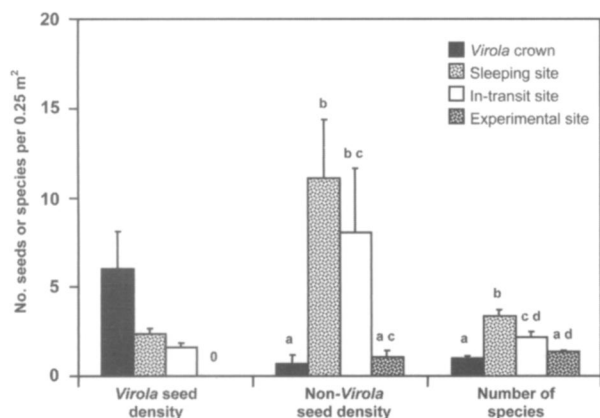


Figure 2. Densities of seeds of *Virola calophylla* (*Virola*), seeds of species other than *V. calophylla* (non-*Virola*), and numbers of species of seeds represented underneath *V. calophylla* crowns (*Virola* crowns; $n = 10$), and at sleeping ($n = 14$), in-transit ($n = 14$) and experimental sites ($n = 132$). Bars depict mean ± 1 SE. Differences among site types are indicated by lower-case letters over bars and were tested using Tukey's studentized range test after a significant Kruskal–Wallis test. Bars without lower-case letters indicate no significant differences among site types.

of non-dispersed seeds (Figure 1), which tended to be at higher densities and, by definition, were beneath *V. calophylla* females. On average, there were 2.1 species of seed (range = 1–11) and 5.3 seeds of species other than *V. calophylla* (range = 0–116) in each quadrat. Both species richness of seeds and the density of non-*Virola* seeds were significantly higher at sleeping and in-transit sites than beneath *V. calophylla* females or at experimental sites (Figure 2). Higher densities of non-*Virola* seeds significantly decreased survival at 16 and 38 d, but had no effect at the end of the study (Table 1). Seeds that were dispersed later in the season had a higher probability of surviving at 38 d, but the effect was even larger by the end of the study (Table 1).

Protected seeds had greater survival than unprotected seeds. Fifty-two per cent of protected seeds (131 of 252 seeds) survived until the end of the study, 45% as germinated and established seedlings and 7% as intact seeds that could have germinated later. The mean time to germination was 335 d. Although a total of 56% of all protected seeds germinated, seedlings from 23% of the seeds that germinated later died. Infected radicles became soft, spongy and brown, compared with healthy radicles, which were turgid and yellowish-green. Ten per cent of all seeds had rotten endosperm, but did not show any apparent penetration of the seed coat.

Of the 48% of protected seeds that died, 43% were killed by scolytid beetles, making these beetles the most important non-vertebrate agent of seed mortality. A total of 20% of all seeds died as a result of beetle infestation when protected from predation by vertebrates. However, this number is unlikely to represent the proportion of unprotected *V. calophylla* seeds killed by beetle infestation

because vertebrate predators, such as spiny rats, tended to find and eat seeds before scolytid beetle eggs were laid and larvae developed. In addition, egg-laying by scolytid beetles did not always result in death of *V. calophylla* seeds, as seeds of several surviving seedlings had the characteristic holes made by scolytid beetles in their seed coats. The probability of a seed dying by the end of the study from infestation by scolytid beetles, relative to all other possible fates, was a decreasing function of the distance from the nearest fruiting *V. calophylla* (analysis of deviance; $\chi^2 = 5.08$, $df = 1$, $P = 0.0241$), but was independent of the density of seeds in the quadrat (analysis of deviance; $\chi^2 = 0.88$, $df = 1$, $P = 0.348$).

DISCUSSION

The spatial pattern of seed deposition generated by spider monkeys had consequences for post-dispersal seed fates, particularly for survival to the seedling stage. Seeds dispersed in clumps at spider monkey sleeping sites had equally low survival as seeds that were never dispersed away from *V. calophylla* females. On the other hand, seeds dispersed in a more scattered pattern (seeds at in-transit sites and those experimentally dispersed) had higher rates of survival. To the extent that experimental sites simulated avian dispersal, *V. calophylla* seeds dispersed by birds would have greater odds of surviving, relative to seeds at sleeping sites or non-dispersed seeds beneath *V. calophylla* females. Seed survival was also negatively dependent upon the local density of *V. calophylla* seeds and positively dependent upon the distance from the nearest female *V. calophylla* tree. These results indicate that Janzen–Connell mechanisms (Connell 1971, Janzen 1970) contributed to some of the variation among dispersal site types, as in-transit sites had low seed density and were distant from females. However, seeds at sleeping sites, which are far from *V. calophylla* females, and non-dispersed seeds had equal survival rates, suggesting that conspecific density- and distance-dependent effects acted independently and did not explain all the variation among dispersal-site types in this system. Instead, other characteristics of the seed shadow generated by spider monkeys also significantly affected seed survival, particularly the high density of non-*Virola* seeds that spider monkeys co-dispersed with *V. calophylla* at sleeping sites. Indeed, survival of *V. calophylla* seeds depended not only on their own density, but on the density of seeds of other species as well. This study therefore highlights the importance of considering seed fate in the context of natural seed deposition patterns.

Factors affecting seed predation and scatter-hoarding

As observed in other large-seeded tropical trees, mortality of unprotected seeds was high (Andresen 1999,

Augspurger & Kitajima 1992, Howe *et al.* 1985, Sork 1987, Terborgh & Wright 1994, Wenny 2000). In contrast, protected seeds had a more than two-times greater chance of surviving, indicating that vertebrate seed predators impose strong selection pressure in the transition from the seed to the seedling stage. A relatively high percentage of protected seeds germinated, but they had a long mean time to germination. Consequently, *V. calophylla* seeds were exposed to predation risk for extended periods. This extended time to germination is likely a result of morphological dormancy in which the embryo is immature when the seed is dispersed, as observed in *V. koschnyi* (Baskin & Baskin 1998). Unprotected seeds with earlier dates of dispersal had significantly reduced odds of surviving, suggesting that this increased duration of exposure risk may have population-level significance.

Spiny rats (*Proechimys* spp.) were important predators of *V. calophylla* seeds at CCBS, in parallel with studies in other neotropical forests (Adler & Kestell 1998, Asquith *et al.* 1997, Forget 1991). A recent study at CCBS also found high rates of seed predation of *Astrocaryum murumuru* (Arecaceae) by spiny rats (Beck & Terborgh 2002). Spiny rats also scatter-hoarded *V. calophylla* seeds, but the infrequency and short dispersal distances of scatter-hoarded seeds suggest that their scatter-hoarding may do little to rearrange seed deposition patterns in this system. A similar conclusion was also reached by Larson & Howe (1987) with respect to the dispersal of *V. nobilis* by agoutis in Panama, which did not prey on seeds, but only moved them short distances to eat the aril. The conclusion that scatter-hoarding by spiny rats may not substantially change the initial deposition pattern of *V. calophylla* seeds should be viewed with caution, as this study did not extend beyond 1 y. The frequency of scatter-hoarding and the survival of scatter-hoarded seeds are likely to vary seasonally and annually (Brewer & Rejmánek 1999, Feer & Forget 2002, Forget 1996) with changes in rodent population densities and resource availability (Adler 1998, Forget *et al.* 2002, Henry 1999). Multi-year investigations are essential for understanding the extent of such variation. Other terrestrial vertebrates, such as agoutis, are also likely to prey upon, cache or disperse *V. calophylla* seeds, as seen in congeners elsewhere (Forget & Milleron 1991, Forget *et al.* 2000, Larson & Howe 1987).

Scolytid beetles in the genera *Coccotrypes* and *Spermophthorus* were also important predators of *V. calophylla* seeds, as observed for other tropical tree species (Hammond *et al.* 1999, Janzen 1972). Insect seed predators have frequently been found to be distance-responsive (Hammond *et al.* 1999, Howe *et al.* 1985). Our results are consistent with these observations because the probability of a seed dying from infestation by scolytid

beetles decreased with distance from the nearest *V. calophylla* female tree.

The significant effects of site characteristics on seed survival as well as variation among dispersal-site types in seed survival are likely mediated by the behaviours of seed predators. Which site characteristics influenced seed survival changed through time, as other studies have also found (Forget *et al.* 2000, Wenny 2000). The significant positive effect of leaf litter depth on early seed survival is consistent with optimal foraging by seed predators experiencing diminishing returns (Charnov 1976, Hughes *et al.* 1995, Kotler *et al.* 2001). Seeds in deeper leaf litter may be missed by foragers or have extra search costs and may therefore escape predation.

Sleeping sites had high densities of seeds and were distant from *V. calophylla* females, yet seeds there had similar survival to those beneath *V. calophylla* females. This result suggests that the effects of conspecific density and distance can independently affect seed survival in this system. Other factors in addition to higher *V. calophylla* seed density likely interact to result in the low survival at sleeping sites. Because sleeping sites are large (Russo & Augspurger 2004), they had higher numbers and higher densities of *V. calophylla* seeds, as well as of other species, than in-transit sites. In addition, sleeping sites had both higher densities of seeds other than *V. calophylla* and species richness of seeds than underneath *V. calophylla* females. Consequently, they constitute a relatively large and diverse food resource that is presumably attractive to generalist seed predators, such as spiny rats.

Together, the negative effect of increasing non-*Virola* seed density and the positive effect of increasing *V. calophylla* seed density on survival to 16 d and 38 d suggest short-term apparent competition. Apparent competition is an indirect interaction that occurs when one prey species negatively affects another prey species because one or both prey species have a positive effect on a predator species (Holt & Kotler 1987). Apparent competition has been observed in studies of the foraging behaviour of granivorous rodents (Brown & Mitchell 1989, Veech 2001). The presence of more preferred non-*Virola* seed species in high density at sleeping sites could cause seeds of *V. calophylla* to be harvested more frequently there than when they are in high-density monospecific patches (under *V. calophylla* females), if seed predators remain in the high-density, multi-species patches (sleeping sites) relatively longer. This interpretation is consistent with the greater survival of *V. calophylla* seeds under *V. calophylla* females at 16 and 38 d, relative to seeds at sleeping sites. Seed predators may also learn the locations of re-used sleeping sites and *V. calophylla* females if they represent reliable resource patches (Lima 1984). Spider monkey dung may also attract seed predators (Andresen 1999),

particularly to re-used sleeping sites. Thus, the benefit of escaping high predation at the parent by being dispersed away from it is reduced for seeds dispersed to sleeping sites.

By the end of the study, however, local density of *V. calophylla* seeds had a strong negative effect on seed survival. Studies modelling rodent foraging based on optimal foraging theory frequently find higher harvest rates with increasing density of patchily distributed seed resources (Mitchell & Brown 1990, Schmidt & Brown 1996, Sih 1984), which accords with the density-dependent seed survival observed here. Survival of *V. calophylla* seeds was also positively distance-dependent, although this effect appeared to be relatively weaker than that of density. However, some studies have failed to find an effect of distance from the nearest conspecific tree on seed predation and scatter-hoarding by vertebrates (Forget *et al.* 2000, Peres *et al.* 1997, Terborgh & Wright 1994). Because predation by scolytid beetles was distance-dependent, it is possible that the distance-dependent seed survival observed here was primarily due to predation by beetle or other seed predators, rather than by spiny rats.

Conclusions

The density-dependence that Janzen (1970) and Connell (1971) initially described as a mechanism for maintaining species diversity involves the density of conspecifics only. However, spider monkeys created a species-rich community of seeds at their sleeping sites, as has been observed in other primates (Julliot 1997). The low survival of *V. calophylla* seeds at sleeping sites should be viewed not only in the context of the high density of *V. calophylla* seeds there, but also the high density of seeds of other species, as well. This study demonstrated that other characteristics of the seed deposition pattern, in addition to conspecific density- and distance-dependence, contributed significantly to variation in seed survival. Therefore, to avoid significant sources of variation in post-dispersal seed fate remaining unexplained, studies of post-dispersal seed fate should directly incorporate data on the characteristics of natural seed deposition patterns.

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